Holocene terrestrial gastropod faunas from Isla Santa Cruz and Isla Floreana, Galápagos: evidence for late Holocene declines

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Abstract. We report 16 species of land snails from late Holocene cave deposits and nearby surface areas on Isla Santa Cruz and Isla Floreana, Galápagos Islands. These snails are associated with vertebrate fossils that accumulated in lava tubes or fissures largely as the regurgitated items of barn owls (*Tyto punctatissima*). Most or possibly all of the snails, however, probably do not represent prey remains, but entered the cave mainly with infilling sediment. The fossil snails represent a much less complete sample of each island's historic fauna than do the vertebrate fossils from the same deposits. Radiocarbon ages on these faunas range from 2420 ± 25 years BP to Modern. Lectotypes and paralectotypes are designated for *Naesiotus nesioticus* and *Naesiotus reibischi*. *Naesiotus galapaganus,* which is rare in historic collections, occurred abundantly in the fossil deposits on Floreana. Five species from these collections on Santa Cruz had not been previously reported from this island (*Gastrocopta duncana, Succinea corbis, Guppya bauri,* and two species of *Naesiotus* that have recently been described elsewhere). As with vertebrates, certain species of snails have suffered considerable late Holocene declines in range and abundance, and possibly have become extinct in Galápagos. The causes of gastropod declines are not clear, but are likely related to human impact of the past century. The most likely cause is habitat destruction by introduced goats, donkeys, and pigs, although predation by introduced rodents may also be important.

INTRODUCTION

Fossils have traditionally played a minor role in studies of the evolution and biogeography in the Galápagos Islands. This is largely because few scientists have looked for them and have regarded the volcanic terrain of Galápagos (Fig. 1) to be a poor environment for the deposition and preservation of fossils. Invertebrate fossils have been reported from localized marine sedimentary rocks in Galápagos (Hertlein 1972 and references therein), but these studies were based upon field work done decades before absolute dating of volcanic rocks was possible through potassium-argon and paleomagnetic determinations. Renewed interest in the Quaternary marine fossils of Galápagos (James 1984, Hickman and Lipps 1985) has resulted from new collections from deposits stratigraphically related to lava flows whose ages are fairly well known.

Until the past several years, the paleontology of terrestrial organisms in Galápagos had received even less attention than that of marine organisms. Again, much of this lack of attention was due to the axiom of geology that states the rarity or lack of fossils in volcanic rocks. Biologists (e.g., Lack 1960) lamented that Galápagos was, unfortunately, an area that had yielded no paleontological clues about the history of the birds

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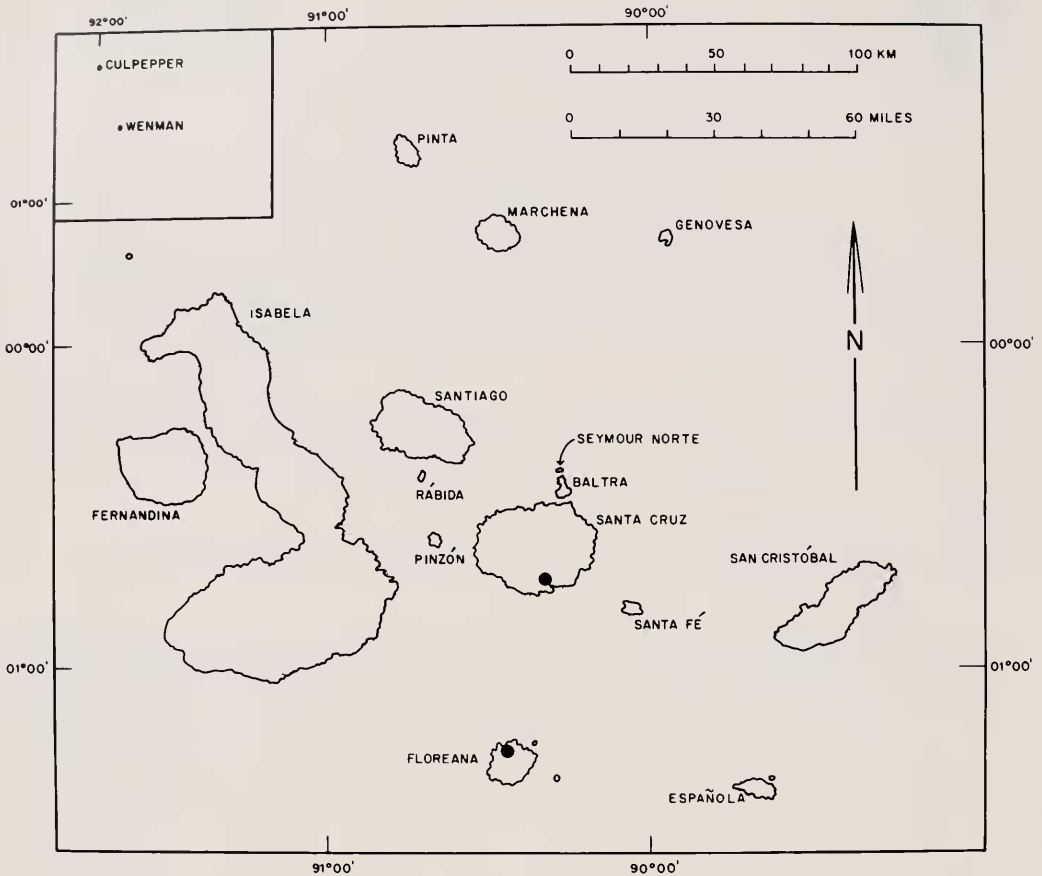
Figure 1.   Galápagos Islands, Ecuador. Dots indicate the approximate locations of the fossil sites on Floreana and Santa Cruz.

or other terrestrial organisms for which these islands are so well known. This situation has now changed.

In 1978 and 1980, DWS collected large samples of fossil vertebrates from Isla Santa Cruz and Isla Floreana (Fig. 1), and a smaller sample from Isabela. In 1984, large collections were made on San Cristóbal, Rábida, and Isabela. Only the collections from Santa Cruz and Floreana yielded large samples of gastropods. The fossil vertebrates from Santa Cruz and Floreana, and to some extent those from Isabela, have been reported (Steadman 1981, 1982, 1985, 1986; Steadman and Ray 1982); from these reports we have abstracted the stratigraphic and chronological context of the fossil snail faunas, supplemented for Santa Cruz by data previously unpublished. Although none of the fossil deposits has been shown to pre-date even the Holocene, the paleofaunas nevertheless shed new light on the natural (=before human contact) distributions of species, and have helped to resolve problems in the systematics of living or recently extinct species.

Late Holocene vertebrate paleofaunas have shown that human-caused predation and habitat degradation have altered natural patterns of distribution and diversity on islands (Pregill and Olson 1981, Olson and James 1982*a, b*, Olson and Hilgartner 1982, Steadman et al. 1984). In Galápagos as well, analyses of vertebrate paleofaunas have revealed much extinction that is related to human impact (Steadman and Ray 1982, Steadman 1986). The present analysis of gastropods from the same fossil sites provides a comparison from an entirely different element of the Galápagos paleofauna.

Site Descriptions and Sampling Methods

The fossil snail collections are mainly from lava tubes or fissures in the arid lowlands. Lava tubes are especially effective repositories for terrestrial sedimentation in Galápagos.

Floreana. — The fossil fauna of Floreana was collected from four caves in the Post Office Bay region in the north-central coast of the island (see figs. 2–3 of Steadman 1986). The elevations of the caves range from 20 to 50 m above modern sea level. No cave is more than 500 m from the present seashore. Access to each cave is through a vertical collapse in the roof created by weathering processes such as pedogenesis, growth of tree roots, and percolation of water. Two of the caves, Cueva de Post Office (Inferior) and Cueva de Post Office (Superior), had been mapped previously by Montoriol-Pous and Escola (1975), who also described various physical and chemical features of the caves. The other two caves, Finch Cave and Barn Owl Cave, had not been mapped or described before our explorations. Fossils were collected from the surface of the floor of each cave, and except in Finch Cave, sediments were also excavated using standard techniques and washed through screens of $\frac{1}{4}$ inch and $\frac{1}{16}$ inch mesh. The species composition of the faunas from excavations did not differ from that of the floor's surface, although, as one would expect, a higher percentage of small species (both of mollusks and vertebrates) was recovered from the screened sediments. Fossils were typically most common near the roof collapse. The sediments from all excavations were generally similar to each other in physical characteristics, consisting of combinations of clays, silts, sands, and gravels that were usually poorly sorted and rather angular. Water and gravity sliding seem to have deposited the sediments, but the poor sorting, poor rounding, and lack of laminations suggest a short distance of transport.

The 20 000 vertebrate fossils from Floreana consist of nearly every resident species of bird, reptile, and mammal, including six species that no longer occur on Floreana: *Geochelone elephantopus* (tortoise), *Alsophis biserialis* (snake), *Tyto punctatissima* (barn owl), *Mimus trifasciatus* (Floreana mockingbird), *Geospiza nebulosa* (sharp-beaked ground-finch), and *G. magnirostris* (large ground-finch). The above species, except *Tyto punctatissima,* are known on Floreana from early 19th century specimens. The loss of each of these species can be related to human activities, especially the settlement of the island in 1832 by several hundred people (Steadman 1986).

Six radiocarbon ages from the Floreana sites (table 2 of Steadman 1986) range from 2420 ± 25 years BP to Modern. Each determination is based upon material from the surface of the floor, as no organic material other than bone and gastropod shells was recovered from the sub-surface. The radiocarbon data indicate that organic material has been accumulating in the Floreana caves for at least the past several thousand years. We cannot say how much older certain of the underlying sediments are, but based upon similarities in faunal composition and in preservation of the bone itself, all excavated materials are probably also late Holocene in age.

Santa Cruz. — As with the paleofaunas of Floreana, the fossil vertebrate faunas from Santa Cruz are derived mainly from regurgitated prey remains of barn owls (*Tyto punctatissima*), and represent a thorough sampling of the vertebrate life of the island before human disruption (Steadman 1986). Fossils were collected from two sites in the arid lowlands of southern Santa Cruz (*see* fig. 2 of Steadman and Ray 1982). The first is Cueva de Iguana, a fissure ca. 10 m deep that trends east–west for at least several hundred meters, parallel to and seaward from the conspicuous fault scarp 400 m north of the Charles Darwin Research Station. The elevation of Cueva de Iguana is only ca. 10 m, and brackish water flows through its bottom. Vertebrate fossils have accumulated in Cueva de Iguana in thin, unstratified pockets of sediment perched on small, horizontal ledges of the roughly vertical walls. Eight such accumulations included land snails.

The second fossil site on Santa Cruz is Cueva de Kubler, a large lava tube 1.5 km north of Puerto Ayora, at ca. 75 m elevation. Cueva de Kubler has been mapped and described by Stoops (1967), Balasz (1972), and Montoriol-Pous and de Mier (1977), none of whom, however, noted the abundance of fossils within the cave. Five exca-

vations were made in the loose, powdery, unstratified sediments of Cueva de Kubler, and fossils were collected from the floor's surface as well. Excavations IIB, IIC, IID, and IIE were in sediments that had been redeposited within the cave. Excavation IIA, whose sediments were the source of those in Exs. IIB–IIE, had not been redeposited. Therefore, unlike in Exs. IIB–IIE, the sediments of Ex. IIA contained fossils only of native fauna, uncontaminated by the remains of two murine rodents (*Rattus rattus* and *Mus musculus*) introduced onto Santa Cruz in historic times. Bones of the introduced rodents occurred on the surface of Ex. IIA, but not within the sediments. Excavation IIA (1.0 m × 3.0 m × 0.8 m deep) was spectacularly fossiliferous, especially in the upper half, whereas Exs. IIB–IIE, which were smaller in volume than Ex. IIA, were very fossiliferous throughout. A very crude estimate of the number of vertebrate fossils from these excavations is several hundred thousands. The sediments of both Cueva de Iguana and Cueva de Kubler are rather poorly sorted silts, clays, and pebbles. Deposition was probably through a combination of water, wind, and gravity sliding.

The vertebrate faunas of Cueva de Iguana and Cueva de Kubler are similar, both being dominated by an extinct rice rat (*Nesoryzomys indefessus*). Two other extinct rodents occur in fair numbers (the smaller rice rat *N. darwini* and the giant thomasomyine rat *Megaoryzomys curioi*). Both species of *Nesoryzomys* became extinct on Santa Cruz in the 20th century, whereas *Megaoryzomys* has never been recorded historically. Each species of terrestrial reptile ever reported from Santa Cruz, including the historically extinct land iguana (*Conolophus subcristatus*), occurs in the sites, as does nearly every species of resident bird.

No radiocarbon ages have been determined for the paleofauna of Cueva de Iguana, but these fossils are undoubtedly late Holocene in age, based upon the loose nature of the sediments and the low level of mineralization of the fossils, some of which are entirely modern in appearance. Several radiocarbon ages have been determined for the Cueva de Kubler paleofauna, but these samples (wood) were badly contaminated with modern radioactive carbon, probably from surface testing of nuclear weapons in the Pacific (R. Stuckenrath in litt.). Unfortunately, therefore, the ages for the Cueva de Kubler samples vary from 1755 ± 335 years BP to 117.5% of Modern. Even the older date probably is contaminated by bomb-produced radiocarbon. Because bones and snails may be less prone to radioactive contamination than plant material, there is still hope of obtaining future determinations that have minimal contamination. Resolution of the chronology of Cueva de Kubler and Cueva de Iguana will depend either upon species-specific radiocarbon dating of bone itself, using tandem accelerator mass spectrometry (such as done recently for plants by Betancourt et al. 1984), or the dating of large quantities of land snails through fairly standard counting techniques, as outlined by Goodfriend and Hood (1983) and Goodfriend and Stipp (1983).

A surface sample of empty snail shells was collected for camparison with the cave samples along the trail to Tortuga Bay on Santa Cruz, ca. 1.5 km south of Cueva de Kubler at ca. 30 m elevation. This locality represents shells that were lying beneath and between large basaltic boulders along the trail.

Systematics

The Galápagos land snail fauna was reviewed by Dall (1896) and Dall and Ochsner (1928). Additional contributions include those of Pilsbry (1897–1898, 1916–1918, 1927–1935), Odhner (1950), A. G. Smith (1966, 1971, 1972, 1974), and Vagvolgyi (1974, 1977). Breure and Coppois (1978) analyzed shell and anatomical features of most of the Galápagos bulimulid species and rejected the subgeneric classification of Dall (1920). These authors also reported on the locations of type material of many Galápagos species and designated lectotypes for some. Breure (1979) gave additional information on the locations of type material in his review of the Bulimulinae. Coppois and Glowacki (1983) used factor analysis to study shell variation among species from Isla Santa Cruz.

This report is based on over 10 000 fossil shells, which have been deposited in the
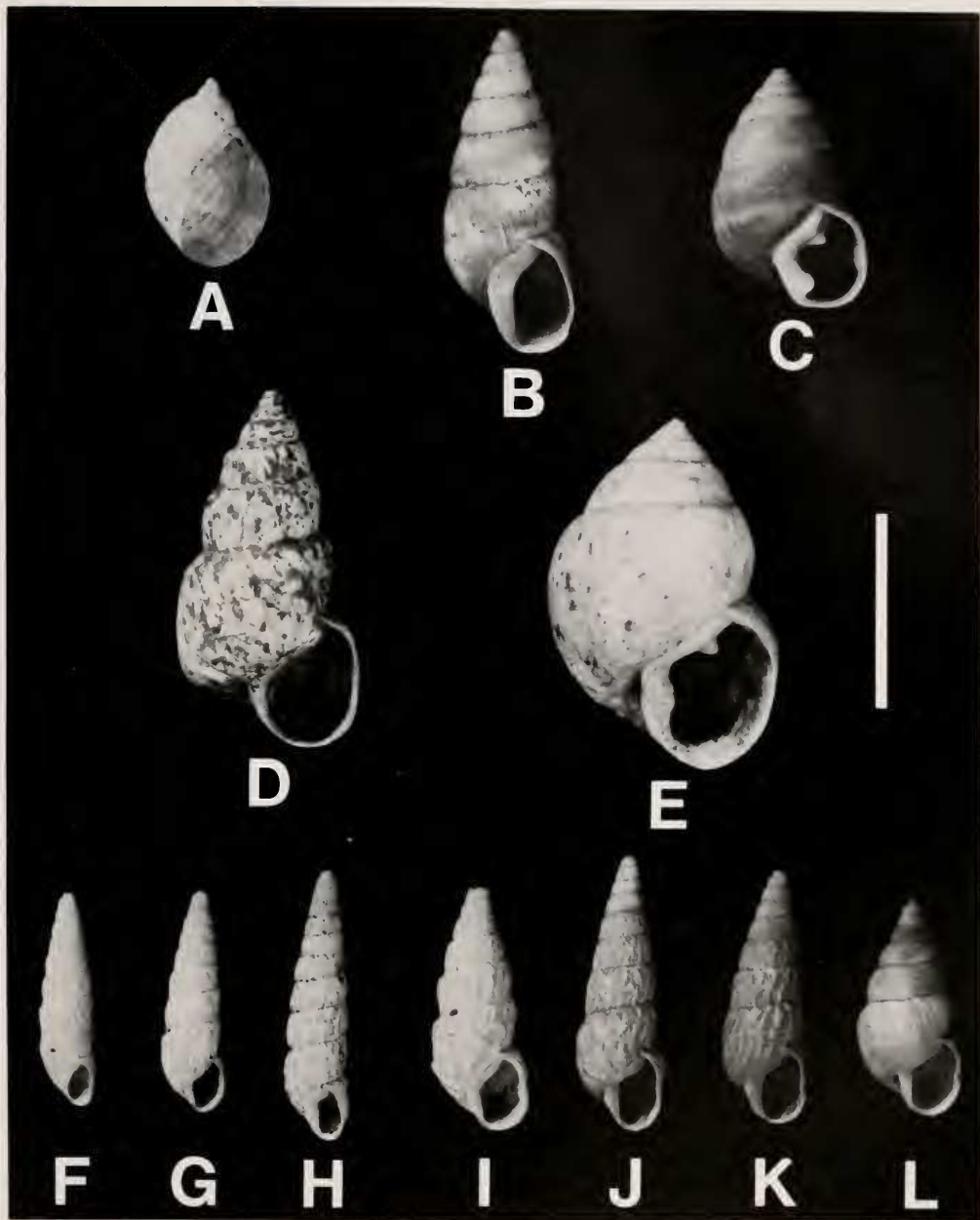
FIGURE 2. Shells of some Galápagos land snails. All except F and I are fossil shells from Isla Santa Cruz or Isla Floreana. A, *Succinea corbis* (USNM 861456) from Cueva de Kubler, Santa Cruz; B, *Naesiotus galapaganus* (USNM 861559) from Barn Owl Cave, Floreana; C, *Naesiotus cymatias* (USNM 861490) from Cueva de Iguana, Santa Cruz; D, *Naesiotus blombergi* (USNM 861505) from Cueva de Kubler; E, *Naesiotus ochsneri* (USNM 861502) from Cueva de Kubler; F, *Naesiotus reibischi* lectotype; G–H, *N. reibischi* (USNM 861532) from entrance to Cueva de Kubler; I, *Naesiotus nesioticus* lectotype; J–K, *Naesiotus nesioticus* from Cueva de Kubler (USNM 861509); L, *Naesiotus kublerensis* holotype from Cueva de Kubler (USNM 842298). Scale bar is 10 mm.

Division of Mollusks, National Museum of Natural History, Smithsonian Institution, Washington, D.C. Species were identified mainly by examination of the published literature and by comparison with the collections of Galápagos gastropods in the Division of Mollusks of the National Museum of Natural History, Washington, D.C.

(specimen catalog numbers indicated by the prefix USNM); the California Academy of Sciences in San Francisco (CAS); the Academy of Natural Sciences of Philadelphia (ANSP); and the Museum of Comparative Zoology of Harvard University (MCZ). Type material was examined for all but three of the species identified from fossils. No attempt was made to revise classification at the generic or familial levels.

Unfortunately, no detailed, comprehensive account has been published on the land snails collected in 1964 during the Galápagos International Scientific Project, now housed mainly at the California Academy of Sciences. A. G. Smith (1966) provided an informative summary, but these collections have not yet been described in detail. A thorough review of this collection and associated field notes would improve our understanding of the habitats occupied by the various species of land snails. The habitat data available in Ochsner's (1905–1906) field notes, R. P. Smith's (1971) unpublished study, and Coppois' (1984) transect study of the northern slope of Santa Cruz are useful but are inadequate to make definitive statements about the range of habitats of land snails, thus limiting our interpretations of the fossil fauna.

Class Gastropoda Cuvier, 1797
Subclass Prosobranchia Milne Edwards, 1848 (=Streptoneura Spengel, 1881)
Order Archaeogastropoda Thiele, 1925
Family Helicinidae Latreille, 1825
Genus *Helicina* Lamarck, 1799
Helicina nesiotica Dall, 1892

Helicina (Idesa) nesiotica DALL, 1892, p. 97.
Sturanya nesiotica (Dall). WAGNER 1905–1911, p. 45.
Helicina nesiotica Dall. A. G. SMITH 1971, p. 7.

Type.—Holotype: USNM 107324. Pl. XV, figs. 1–2, in Dall (1896). Type locality is Chatham (San Cristóbal) Island at 1600 feet (488 m) above sea level (Dall 1892).

Material.—USNM 861375–861395 (Santa Cruz), USNM 861396 (Floreana).

Remarks.—Two species of *Helicina* have been described from Galápagos, both by Dall (1892, 1917). *Helicina nesiotica* is based on a specimen from Isla San Cristóbal (Chatham). Dall's descriptions (1892, 1896) of this species refer to its "bright reddish chestnut epidermis" or periostracum. Dall described *Helicina ochsneri* Dall, 1917 from material (type: USNM 216021) from Isla Isabela (Albemarle). He described this species' periostracum as "blackish," but noted that removal of the periostracum of *H. ochsneri* exposed a shell with a surface and color similar to *H. nesiotica*.

All the fossil *Helicina* lack the periostracum, so their identification as *H. nesiotica* is based on the sizes of the fossil specimens. Shell height/diameter for *H. nesiotica* is 3.3 mm/2.3 mm (Dall 1892) and for *H. ochsneri* is 4.7 mm/3.5 mm (Dall 1917). Some fossil individuals approach the measurements stated for *H. ochsneri* and may belong to that species.

Dall and Ochsner (1928) reported *H. nesiotica* from Floreana. Based on examination of CAS material and the holotype, the *Helicina* reported from Santa Cruz by A. G. Smith (1966) is *H. nesiotica*.

Subclass Pulmonata Cuvier, 1817 (=Euthyneura Spengel, 1881, in part)
Order Stylommatophora A. Schmidt, 1856
Family Achatinellidae Gulick, 1873
Subfamily Tornatellininae Pilsbry, 1910
Genus *Tornatellides* Pilsbry, 1910
Tornatellides chathamensis (Dall, 1892)

Leptinaria chathamensis DALL, 1892, p. 98.
Tornatellina chathamensis (Dall). DALL 1900, p. 95.
Tornatellides chathamensis (Dall). ODHNER 1950, p. 254.

Types.—USNM 107322 (6 syntypes). One specimen in Pl. XVI, fig. 9, of Dall

(1896). Type material was taken on ferns at 1600–2000 feet (488–610 m) above sea level on Chatham (San Cristóbal) Island.

Material. — USNM 861397–861403 (Santa Cruz).

Remarks. — Placement of this species in *Tornatellides* and the subfamily Tornatellininae of the family Achatinellidae follows Cooke and Kondo (1960). Vagvolgyi (1974) noted that *Tornatellides chathamensis* and *Nesopupa galapaganus* Vagvolgyi, 1974 represent the only Indo-Pacific elements in the Galápagos land snail fauna, which is otherwise Neotropical in origin.

Cooke and Kondo (1960:246) observed that individuals in two lots in the Bishop Museum (BPBM 115299 from Chatham [San Cristóbal] Island and BPBM 115300 from Albemarle [Isabela] Island) are not as sharply conical as the specimen figured by Dall (1896, Pl. 16, fig. 9). SMC compared the fossil specimens with the syntypes (USNM 107322), finding that the fossils likewise are less conical than the figure and syntypes.

Dall (1896) included *Bulimulus (Pelecostoma) cymatoferus* Reibisch, 1892 in his synonymy for this species. Dall's name was published earlier in 1892 and therefore has priority. Our examination of Reibisch's (1892) description and figure suggest that Dall's assessment was correct, although we have not seen Reibisch's type material (see comments below on types of *Gastrocopta clausa*).

Smith (1966) first reported *Tornatellides* from Santa Cruz.

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Family Pupillidae Turton, 1831
Genus *Gastrocopta* Wollaston, 1898
Gastrocopta duncana Pilsbry, 1931

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Gastrocopta duncana PILSBRY, 1931, p. 65–66, Pl. 17, figs. 1–2.

Types. — ANSP 152689 includes the lectotype designated by Baker (1963) and 3 paralectotypes. Additional paralectotypes: ANSP 152690 (8 shells) and ANSP 152691 (5 shells). Pilsbry (1931) reported that the 17 specimens of the type material were collected with *Gastrocopta clausa* on the south side of Duncan (Pinzón) Island. He stated that these localities were from 500 feet (152 m) elevation to the summit (457 m), with *G. duncana* being more abundant at the summit.

Material. — USNM 861404 (Santa Cruz).

Remarks. — A single specimen from the trail near Cueva de Kubler, Santa Cruz, represents the first record of this species outside of Isla Pinzón.

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Gastrocopta clausa (Reibisch, 1892)

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Pupa (Leucochila) clausa REIBISCH, 1892, p. 15.
Gastrocopta clausa (Reibisch). PILSBRY 1916, p. 99.

Types. — The location of Reibisch's type material for this species is not known to us, although Breure (1979) reported that some of Reibisch's bulimulid type material is in the British Museum (Natural History) and the Zoologisches Museum der Humboldt-Universität in Berlin. Reibisch's (1892) description includes a figure (Pl. II, fig. 10) and a description of the type locality as shrubs near the sea, Indefatigable (Santa Cruz) Island.

Material. — USNM 861405–861426 (Santa Cruz), USNM 861427–861440 (Floreana).

Remarks. — Pilsbry (1931:69) considered *Gastrocopta clausa* to be very similar to but distinct from *Gastrocopta munita* (Reibisch, 1892), the former having a well developed subcolumellar tooth that is either absent in *G. munita* or very weakly tuberculate, consisting only of a sloping callus. Later, Pilsbry (1931:71 and pl. 17) referred to specimens of *G. clausa* from Chatham (San Cristóbal) Island that lacked this subcolumellar tooth. These observations plus LaRochelle's (1983) report of apparent intraspecific variation in tooth number among some North American pupillids lead us to question the reliability of this character for separating these two species. The other character that Pilsbry used to separate these species, the presence of a nodule associated

with the parietal lamella that is present in his "typical" *G. clausa,* but absent in *G. munita,* also seems deficient as a diagnostic character. The fossils are identified as *G. clausa* because of the presence of a subcolumellar lamella, expressed to varying extents, and the lack of any other apparent and consistent variation among them. A revision of the Galápagos *Gastrocopta,* a preliminary version of which was very briefly described in an abstract by Vagvolgyi (1979), could resolve some of the confusion concerning these forms.

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Family Succineidae Beck, 1837
Genus *Succinea* Draparnaud, 1801
Succinea corbis Dall, 1893
Figure 2A

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Succinea corbis DALL, 1893, p. 55.

Types. — USNM 107321 (13 syntypes). Pl. XV, fig. 5, of Dall (1896). The type locality is Albemarle (Isabela) Island.

Material. — USNM 861441–861465 (Santa Cruz).

Remarks. — Species identifications based on shell material alone must be considered tentative in this difficult family. The fossil *Succinea* are referred to *S. corbis* because they possess the fine microsculpture that Dall (1893) described as "an excessively fine network of closely reticulated fine incised lines." Dall and Ochsner (1928) later stated that the "lattice-like corrugation" had disappeared from the type material owing to contraction of the periostracum. SMC has examined the syntypes and found this microsculpture to be seen easily under 30× magnification.

Expression of the fine microsculpture ranges from strong to faint. The fine microsculpture was not visible on some of the smaller or more eroded shells. These were identified as *S. corbis* because they differed in no other way from the microsculptured shells in the same lots, although it cannot be ruled out that some or all of these are *Succinea bettii* Edgar Smith, 1877. The specimen (USNM 107318) that Dall (1896, Pl. XV, fig. 6) apparently portrayed as an example of *S. bettii* shows the *S. corbis*-like microsculpture on unworn outer surfaces of the shell and is considered here to be *S. corbis.* We have not examined the type material of *S. bettii*; it is probably in the British Museum (Natural History) [BM(NH)], where Edgar Smith was keeper of mollusks. Examination of this material for microsculptural features would aid in determining whether *S. bettii* and *S. corbis* are synonyms.

A similar pattern of microsculpture is present in two shells (USNM 163056 and USNM 216030) from Cocos Island, Costa Rica, although the overall shell form of these individuals is very short-spired and therefore distinct from *S. corbis.* Another example may be that referred to as "crisscross" sculpture by Solem (1959) in his discussion of Quick's (1939, 1951) work on some Austromalayan *Succinea.*

This is the first record for *Succinea corbis* on Santa Cruz.

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Family Bulimulidae Tryon, 1867
Genus *Naesiotus* Albers, 1850

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Remarks. — The full generic status of *Naesiotus,* including the Galápagos species, has been recognized by A. G. Smith (1971, 1972, 1974), Vagvolgyi (1977), Breure and Coppois (1978), and Breure (1979), although Coppois and Glowacki (1983) recognized *Naesiotus* as a subgenus of *Bulimulus.*

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Naesiotus galapaganus (Pfeiffer, 1854)
Figure 2B

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Bulimus galapaganus PFEIFFER, 1854, p. 58.
Bulimulus (Naesiotus) galapaganus (Pfeiffer). DALL 1896, p. 435 [synonymy].
Naesiotus galapaganus (Pfeiffer). BREURE AND COPPOIS 1978, p. 176.

Types. — Lectotype [BM(NH) 1975146] and paralectotype [BM(NH) 1975147] designated by Breure and Coppois (1978) (not seen). Pfeiffer (1854) listed the type locality only as the "Galapagos Islands."

TABLE 1. Measurements of shells of some adult *Naesiotus*. Ranges are within parentheses. Specimens are from Santa Cruz unless otherwise indicated.

Specimens	Sample size	Shell height in mm	Terminal apical angle in degrees
Naesiotus nesioticus:			
Lectotype	1	13.2	26
Paralectotypes	3	12.8	26.7
		(11.6–14.7)	(22–31)
USNM 215982	5	13.0	24
		(11.6–13.7)	(22–26)
Trail to Tortuga Bay	4	12.6	23.8
		(11.6–13.1)	(22–26)
Cueva de Kubler surface	2	12.6	21.5
		(12.3–12.8)	(20–23)
Cueva de Kubler Excavation IIA	24	13.2	23.3
		(12.3–17.3)	(20–27)
Cueva de Kubler Excavation IIB	9	12.9	23.1
		(11.5–14.0)	(18–26)
Cueva de Kubler Excavation IIC	4	13.2	23
		(12.8–13.5)	(22–44)
For all *N. nesioticus* above	52	13.0	23.5
		(11.5–17.3)	(18–31)
Naesiotus reibischi:			
Lectotype	1	10.9	15
Paralectotype	1	9.6	17
USNM 534106 (James Island)	3	11.4	15.3
		(10.9–11.9)	(15–16)
Cueva de Iguana	12	11.8	16.2
		(10.9–13.1)	(14–17)
Cueva de Kubler surface	18	11.8	16.2
		(10.5–13.3)	(13–18)
Cueva de Kubler Excavation IIA	2	12.4	17.5
		(12.2–12.6)	(17–18)
For all *N. reibischi* above	37	11.7	16.2
		(9.6–13.3)	(13–18)
Naesiotus kublerensis:			
Holotype	1	10.9	36
Paratypes:			
Cueva de Kubler surface	24	11.0	34.3
		(10.1–12.2)	(30–40)
Cueva de Kubler Excavation IIA	1	11.4	29
Naesiotus duncanus holotype	1	18.9	50
Naesiotus hirsutus holotype	1	9.9	44
Naesiotus cavagnaroi MCZ paratypes	6	21.6	56
		(19.8–23.2)	(51–62)

Material. —USNM 861551–861613 (Floreana).

Remarks. —We are not aware of any published records of this species since Dall (1896) reported it among the collections made by G. Baur in 1890. This species was found in large numbers in all fossil deposits sampled on Florcana.

Naesiotus cymatias (Dall, 1917)
Figure 2C

Bulimulus (*Naesiotus*) *cymatias* DALL, 1917, p. 380.
Naesiotus cymatias (Dall). BREURE 1979, p. 69.

Type. —CAS 1667 (not seen). Photograph in Dall and Ochsner (1928: fig. 19). The type locality is described by Dall (1917) as "Indefatigable [Santa Cruz] Island, under lava blocks in a moist area between 400 and 600 feet [122 and 183 m] elevation."
Material. —USNM 861474–861498 (Santa Cruz).

Naesiotus ochsneri (Dall, 1917)
Figure 2E

Bulimulus (Naesiotus) ochsneri DALL, 1917, p. 38.
Naesiotus ochsneri (Dall). A. G. SMITH 1972, p. 12.

Types.—Holotype: CAS 1668; fig. 20 in Dall and Ochsner (1928). Paratypes: CAS 1490 (3 shells); CAS 1669 and 1670 (one shell each) are labeled as "syntypes"; USNM 215932 (ten shells) labeled as paratypes and with collection data identical to that accompanying Dall's description. The type locality is described as "Indefatigable Island, under lava blocks at 200 to 650 feet [61 to 198 m]" (Dall 1917).
Material.—USNM 861449–861504 (Santa Cruz).

Naesiotus nesioticus (Dall, 1896)
Figure 2I–K

Bulimulus (Naesiotus) nesioticus DALL, 1896, p. 443.
Bulimulus (Naesiotus) naesioticus [sic] Dall, DALL 1920, p. 121.
Naesiotus nesioticus (Dall). BREURE 1979, p. 70.

Types.—USNM 107277 (Fig. 2I) is here designated the lectotype. This specimen was figured by Dall (1896, Pl. XVI, fig. 1) with the original description. A printed label with the specimen indicates that it is the figured "type." The protoconch is mostly missing. Measurements of the four specimens of USNM 107277a, here designated paralectotypes, are presented in Table 1. The type locality is James Island (Isla Santiago).
Material.—USNM 861506–861529 (Santa Cruz).
Remarks.—This species is further discussed below with *Naesiotus kublerensis*.

Naesiotus reibischi (Dall, 1895)
Figure 2F–H

Bulimulus (Naesiotus) Reibischii DALL, 1895, p. 26.
Bulimulus (Naesiotus) Reibischi Dall. DALL 1896, p. 444 [emendation].
Naesiotus reibischi (Dall). BREURE AND COPPOIS 1978, p. 183.

Types.—The shell (USNM 107279) depicted in Pl. XVI, fig. 4, of Dall (1896) and Figure 2F of this paper is here designated the lectotype. This specimen's label indicates that it is the figured "type." USNM 107279a, apparently the second specimen mentioned by Dall (1895:127) in the type lot, is here designated a paralectotype. Some measurements of these specimens are presented in Table 1. The type locality is Indefatigable Island (Isla Santa Cruz).
Material.—USNM 861530–861550 (Santa Cruz).
Remarks.—The long, slender fossil bulimulids are identified here as either *N. nesioticus* or *N. reibischi* (Fig. 2F–K). Coppois and Glowacki (1983) reported two additional slender species, which they referred to as unidentified, from Santa Cruz (see remarks on *Naesiotus kublerensis*). Another long, slender species, *Naesiotus rugiferus* (Sowerby, 1833), has been reported from Santa Cruz by R. P. Smith (1971) and Breure and Coppois (1978). Coppois and Glowacki described the apical sculpture of their two unidentified species and *N. nesioticus* as undulating riblets. Breure and Coppois (1978) described the protoconchal sculpture of *N. rugiferus* as undulating and *N. reibischi* as straight. Examination of the protoconchs of our material and the USNM types revealed that the riblets are straight in the type material of both *N. reibischi* and *N. nesioticus*. This feature could not be discerned reliably in most of our fossil material; the riblets were mostly straight when visible, with some waviness in a few individuals, especially material here referred to *N. reibischi*. The slight variation observed in this feature in the fossil shells provides no basis for referring them to species other than *N. reibischi* and *N. nesioticus*. *Naesiotus reibischi* is further discussed in the comments below on *Naesiotus kublerensis*.

Naesiotus blombergi (Odhner, 1950)
Figure 2D

Bulimulus blombergi ODHNER, 1950, p. 255.
Naesiotus deroyi A. G. SMITH, 1972, p. 9.
Naesiotus blombergi (Odhner). A. G. SMITH 1974, p. 67.

Types. — Breure (1979:68) indicated that a holotype was in the Swedish State Museum of Natural History (Naturhistoriska Riksmuseet) in Stockholm. We are not aware of any published designation of a lectotype for this species. In the original description, Odhner (1950) indicated that 12 specimens constituted the type material and described the type locality as being "200–300 m above sea level on plants, bushes, and trees" on Isla Santa Cruz. That description included figures (Figs. 1, 3–5) of an apertural view of the shell of a single specimen and of apical sculpture, jaw, and radula.

A. G. Smith (1972) designated CAS 13730 as the holotype of *N. deroyi*. He also designated 72 paratypes, which he indicated that he had distributed to various museums and private collections. These paratypes include the 4 alcohol-preserved specimens of MCZ 280009 and 4 dry specimens of USNM 735981, all of which were examined in the present study. Smith's type material was taken on a thorny bush at 264 m elevation on the northwest side of Isla Santa Cruz.

Material. — USNM 861505 (Santa Cruz).

Naesiotus kublerensis Chambers, 1986
Figure 2L

Naesiotus kublerensis CHAMBERS, 1986, p. 289.

Types. — Holotype (USNM 842298) and paratypes (USNM 842299, 7 shells; USNM 842300, 1 shell; USNM 842301, 7 shells; USNM 842302, 5 shells; USNM 842303, 25 shells) from the entrance of or within Cueva de Kubler, Santa Cruz (Chambers 1986). Figure 2L is of the holotype. Paratypes in figure 3 of Chambers (1986) include two shells from USNM 842299 and three shells from USNM 842301.

Material. — USNM 842298–842304 (Santa Cruz).

Remarks. — Among the several, high-spired *Naesiotus* species reported from Santa Cruz are two "unidentified" species reported by Coppois and Glowacki (1983), whose work represents an important quantitative comparative study of Santa Cruz bulimulids. Assigning names to our three elongate species of fossil *Naesiotus* (*N. reibischi, N. nesioticus,* and *N. kublerensis*) and comparison with the available data on Coppois and Glowacki's unidentified species necessitated a more detailed analysis (described below) using the method developed by those authors. In this analysis, the elongate species are compared with respect to two measurements: shell height and terminal apical angle. Coppois and Glowacki (1983) concluded from factor analysis of seven measurements that these two measurements defined intraspecific variation well enough that in most cases an individual bulimulid shell from Santa Cruz could be assigned to a species simply by taking these two measurements and comparing them to those of known samples of only five shells per species, as portrayed in their Figure 3.

In the present study, these two characters were determined (to the nearest .1 mm or the nearest whole degree) for shells of *N. nesioticus, N. reibischi, N. kublerensis,* and to available type material for these and other species, following the methods of Coppois and Glowacki. These data are summarized in Table 1 and Figure 3.

Three major clusters (represented by triangles, circles, and squares, respectively) of points are discernable in Figure 3. The most discrete of these consists of shells here considered as representing *N. reibischi* (squares) and including the type material for that species. This cluster overlaps the coordinates representing Coppois and Glowacki's unidentified species "22" and "56" and is disjunct from their values for *N. reibischi*. In the absence of further information on species "22" and "56," and based on the coordinates of the type material, we refer these very slender shells to *N. reibischi.*

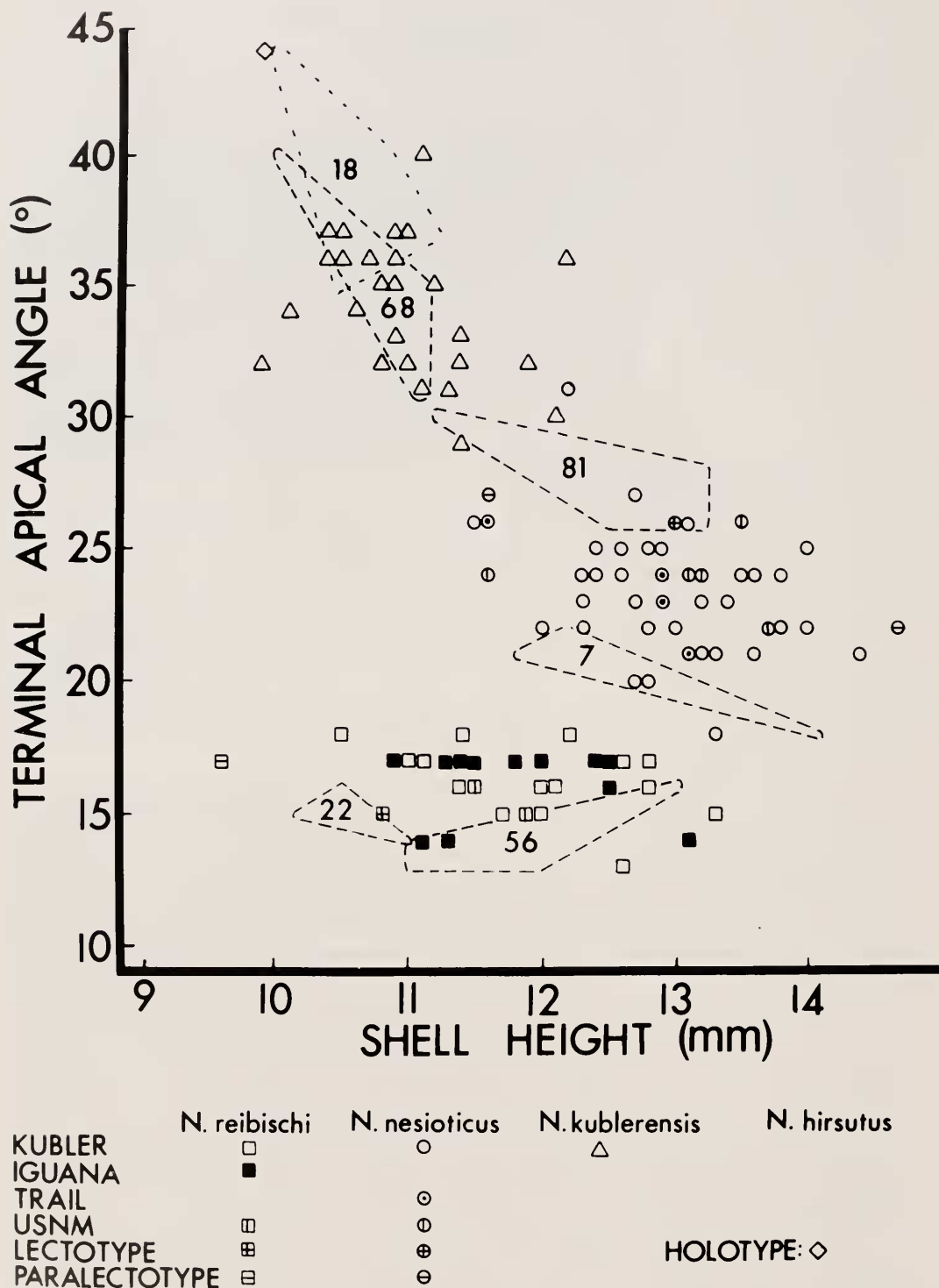The cluster representing our material of *N. nesioticus* (circles) overlaps Coppois

FIGURE 3. Variation in two characters in some elongate *Naesiotus*. Each symbol may represent more than one individual. Numbered areas enclosed by dashed lines were drawn after fig. 3 of Coppois and Glowacki (1983) and delimit their ranges of these measurements for *N. reibischi* (7), *N. hirsutus* (18), *N. jacobi* (68), *N. nesioticus* (81), and two unidentified species of *Naesiotus* (22 and 56). Shells are from Isla Santa Cruz, except the type and "USNM" material of *N. nesioticus*.

and Glowacki's coordinates for both *N. reibischi* and *N. nesioticus.* These are identified here as *N. nesioticus* because this cluster includes the lectotype of *N. nesioticus* and is disjunct from the *N. reibischi* type material. Most shells in this cluster are more slender than the lectotype. We do not believe that this cluster represents common ancestors of *N. reibischi* and *N. nesioticus* because it includes non-fossil material. In addition, neither character is correlated with depth in fossil deposits. As discussed above in the remarks on *N. reibischi,* the differences between *N. reibischi* and *N. nesioticus* in apical sculpture of the shell cited by Coppois and Glowacki (1983) are not supported by the type material.

The third cluster (triangles) represents *Naesiotus kublerensis* and includes a wider range of values for terminal apical angle, but a narrower range for shell height, than the other two clusters. A lectotype of *N. nesioticus* is found near the edge of this cluster, which also overlaps Coppois and Glowacki's (1983) coordinates for *Naesiotus hirsutus* Vagvolgyi, 1977 and *Naesiotus jacobi* (Sowerby, 1883). *Naesiotus kublerensis,* however, possesses axial sculpture that becomes rugose on the body whorl, which is not found on either *N. jacobi* or *N. hirsutus* (Chambers 1986).

The failure of some type material to fall within Coppois and Glowacki's circumscribed boundaries for the corresponding species led us to measure these two characters in additional available *Naesiotus* type material. Coordinates representing the type of *Naesiotus duncanus* (Dall, 1893), the paralectotype of *N. reibischi,* and some MCZ paratypes of *Naesiotus cavagnaroi* A. G. Smith, 1972, fall outside the limits circumscribed for these species by Coppois and Glowacki (1983). The lectotypes of *N. nesioticus* and *N. reibischi* fall within the limits set by Coppois and Glowacki, but the two paralectotypes of *N. nesioticus* fall outside. Although Coppois and Glowacki (1983: 215–216) found that five specimens for each species adequately described the range of variation of larger samples for the species that they studied, their samples did not encompass the variation in all type material and in our material of *N. nesioticus* and *N. reibischi.*

Naesiotus steadmani Chambers, 1986

Naesiotus steadmani CHAMBERS, 1986, p. 287.

Types. —The holotype (CAS 059358) and 67 paratypes (CAS 038052) are shells collected under lava rocks on a cliff above Academy Bay, Santa Cruz. Figure 1 of Chambers (1986) portrays the holotype and three paratypes.

Material. —USNM 842297 (Santa Cruz).

Remarks. —The single fossil specimen (*see* fig. 1 of Chambers 1986) resembles *N. cymatias,* but has a higher spire than that species. It is more weathered in appearance than most of the other fossil shells. The type material was collected on Santa Cruz, but not identified, by A. G. Smith in 1964.

Family Helicarionidae Godwin-Austen, 1888
Genus *Guppya* Mörch, 1867
Guppya bauri (Dall, 1892)

Zonites (Hyalinia) Baueri DALL, 1892, p. 98.
Trochomorpha bauri (Dall). DALL 1896, p. 447 [emendation].
Guppya bauri (Dall). DALL 1900, p. 92.

Type. —USNM 107317. Pl. XV, figs. 8–9 in Dall (1896). The type, which for many years was the only known specimen, was found on "South Albemarle [Isabela] Island on weathered bones of tortoises" (Dall 1892).

Material. —USNM 861466–861467 (Santa Cruz).

Remarks. —Baker (1941:223) suggested that this species may belong in the genus *Habroconus* Fischer and Crosse. This species has been reported from Española, Pinzón, Isabela, and Pinta (Dall and Ochsner 1928), but not previously from Santa Cruz.

Genus *Habroconus* Fischer and Crosse, 1872
Habroconus? *galapaganus* (Dall, 1893)

Conulus galapaganus DALL, 1893, p. 55.
Euconulus galapaganus (Dall). DALL AND OCHSNER 1928, p. 175.
Habroconus? *galapaganus* (Dall). A. G. SMITH 1971, p. 7.

Types.—USNM 107315 (three syntypes), Pl. XV, fig. 11 in Dall (1896). Type locality is described on the label of the syntypes as the southwestern end of Chatham Island (San Cristóbal) at 1600 feet (488 m).

Material.—USNM 861468 (Santa Cruz).

Remarks.—Baker (1941:223) commented that this species may also belong in *Habroconus,* a suggestion apparently followed by Vagvolgyi (1975, Table 4). A. G. Smith (1966) reported *Euconulus* (=*Habroconus*?), probably this species, from Isla Santa Cruz.

Family Zonitidae Mörch, 1864
Genus *Retinella* Fischer *in* Shuttleworth, 1877
Retinella? *chathamensis* (Dall, 1893)

Hyalinia chathamensis DALL, 1893, p. 54.
Vitrea chathamensis (Dall). DALL 1896, p. 448.
Retinella? *chathamensis* (Dall). A. G. SMITH 1971, p. 7.

Type.—USNM 107316. Pl. XV, figs. 3, 10 in Dall (1896) appear to be illustrations of the type. Dall (1893) described the type locality as 1600 feet (488 m) on Chatham (San Cristóbal) Island.

Material.—USNM 861469–861473 (Santa Cruz).

Remarks.—Although reported from a number of islands in Galápagos (Dall and Ochsner 1928), this species had not been recorded on Santa Cruz until A. G. Smith's 1966 report.

DISCUSSION

Distribution of species in fossil deposits.—Only three species were found as fossils at the Floreana localities (Table 2). Two of these, *Helicina nesiotica* and *Gastrocopta clausa,* are small species more commonly recorded from screened excavations than from hand-picked surface remains. *Naesiotus galapaganus* is extremely abundant in

TABLE 2. Fossil land snails from Floreana. X indicates the presence of the species.

	Helicina nesiotica	*Gastrocopta clausa*	*Naesiotus galapaganus*
Cueva de Post Office (Superior)			
Surface		X	X
Excavation 1			X
Excavation 2			X
Excavation 3		X	X
Excavation 4			X
Cueva de Post Office (Inferior)			
Surface		X	X
Excavation 1		X	X
Excavation 2			X
Excavation 3			X
Barn Owl Cave			
Surface			X
Excavation	X	X	X
Finch Cave			
Surface			X

TABLE 3. Land snails from Cueva de Iguana, Santa Cruz. Numbers in Tables 3–6 indicate the minimum number of individuals represented by the fossil material.

	Site 3	Site 4E	Site 4E Area A	Area B	Site 4W Ledge 1	Site 5E Area B	Site 5W Ledge 2	Site 6E
Helicina nesiotica					1			
Tornatellides chathamensis								
Gastrocopta duncana								
Gastrocopta clausa			1		1			
Succinea corbis	5	2	1	6	5		1	2
Naesiotus cymatias	11	6	9	14	12	10	9	28
Naesiotus ochsneri								
Naesiotus nesioticus								
Naesiotus reibischi	4	1	2	4	7	2	4	7
Naesiotus blombergi								
Naesiotus kublerensis								
Naesiotus steadmani								
Guppya bauri								
Habroconus? galapaganus								
Retinella? chathamensis								

all Floreana samples, although this Floreana endemic has only rarely been collected before.

On Santa Cruz, *Naesiotus cymatias* was by far the most common species found in excavations. Thousands of shells of this species were recovered from the excavations in Cueva de Kubler and Cueva de Iguana. *Tornatellides chathamensis, Succinea corbis,* and *Naesiotus reibischi* were also found at all sites, but in lesser numbers.

Only four species were recovered from Cueva de Iguana (Table 3). In contrast to the Kubler excavations, *Naesiotus reibischi* was found in Cueva de Iguana in the absence of *N. nesioticus*. Species composition was similar for all sites within Cueva de Iguana, except that *Helicina nesiotica* was recovered only from Site 4W.

All 14 species from excavations on Santa Cruz were found in Cueva de Kubler (Tables 4–6). A notable feature of the Kubler fauna is the abundance of *N. nesioticus,* which was not found at Cueva de Iguana. The similar, high-spired species *N. reibischi* was also present, but in smaller numbers. Samples of shells taken from the surface of soil deposits among boulders both just outside and within the cave entrance also

TABLE 4. Land snails from entrance and Excavation IIA in Cueva de Kubler (except column under "Trail"), Santa Cruz. The Trail site represents a surface collection of shells from beneath boulders.

	Trail	Surface: near entrance	Entrance rubble	Excavation IIA 0–20 cm	20–40 cm	40–60 cm	60–80 cm
Helicina nesiotica	3	7	16	111	1		16
Tornatellides chathamensis	1		1	3	3		1
Gastrocopta duncana	1						
Gastrocopta clausa	3	38	6	48	6	1	1
Succinea corbis	1	26	18	21			2
Naesiotus cymatias	171	~1000	159	~2200	246	74	19
Naesiotus ochsneri							
Naesiotus nesioticus	21		2	107	1	1	
Naesiotus reibischi		91	21	6			
Naesiotus blombergi							
Naesiotus kublerensis	1	38		9			
Naesiotus steadmani							
Guppya bauri				1			
Habroconus? galapaganus							
Retinella? chathamensis				1			1

TABLE 5.   Land snails from Cueva de Kubler, Excavation IIB, Santa Cruz.

	Surface	0–6 cm	6–12 cm	12–18 cm	18–24 cm	24–30 cm	30–36 cm
Helicina nesiotica	3	399	3	3	1	7	
Tornatellides chathamensis							
Gastrocopta duncana							
Gastrocopta clausa		4	6	2		11	
Succinea corbis		10	2		2		
Naesiotus cymatias	109	~1100	~600	433	339	403	73
Naesiotus ochsneri		1			3		
Naesiotus nesioticus	9	70	23	17	7	10	5
Naesiotus reibischi		4	1	1	2	4	
Naesiotus blombergi					1		
Naesiotus kublerensis							
Naesiotus steadmani							
Guppya bauri							
Habroconus? galapaganus							
Retinella? chathamensis	1	10					

contained both species, but *N. reibischi* was by far the more common. This is curious because these samples were taken from places that would seem to be source areas for snail shells washed into Cueva de Kubler after severe rains. We believe, however, that the snails are from the immediate catchment basin and have not been transported from other habitats. The sample of shells from the trail to Tortuga Bay (collected from the surface of soil deposits among boulders, just as in the surface sample from outside Cueva de Kubler) contained *N. nesioticus,* but not *N. reibischi.* Of these two species, the more common one (*N. nesioticus*) in the Kubler fossil sites and in the surface site near the trail to Tortuga Bay (downslope from Cueva de Kubler) is less common at and near the entrance of Cueva de Kubler. The absence of *N. nesioticus* from the Cueva de Iguana sites may indicate vegetational preference, because Cueva de Iguana is about 65 m lower in elevation than Cueva de Kubler, and one of us (DWS) has observed that the area around Cueva de Iguana lacks several species of woody plants that are common near Cueva de Kubler.

   Naesiotus kublerensis was found only in the surface samples from near the trail to Tortuga Bay and near the entrance to Kubler, and in the top level of Kubler Excavation IIA. It is absent from deeper levels of IIA and from other excavations in Kubler and the Iguana sites.

TABLE 6.   Land snails from Cueva de Kubler, Excavations IIC and IIE, Santa Cruz.

	Excavation IIC					Excavation IIE	
	0–6 cm	6–12 cm	12–18 cm	18–24 cm	24–30 cm	20–30 cm	30–40 cm
Helicina nesiotica	9	100				9	24
Tornatellides chathamensis					1		
Gastrocopta duncana							
Gastrocopta clausa						28	53
Succinea corbis	1		1			2	7
Naesiotus cymatias	2	9	12	6	9	~500	~500
Naesiotus ochsneri		1		1		9	3
Naesiotus nesioticus	3	8	4	3	6	12	21
Naesiotus reibischi		1				1	
Naesiotus blombergi							
Naesiotus kublerensis							
Naesiotus steadmani						1	
Guppya bauri							2
Habroconus? galapaganus							1
Retinella? chathamensis						1	

Twelve of the 17 shells of *N. ochsneri* were found in Kubler Excavation IIE. The five additional shells were found in Excavations IIB and IIC. Strangely, this species was absent from Excavation IIA, whose sediments represent the source area for the sediments of Excavations IIB and IIC. This is significant because only Excavation IIA is uncontaminated by post-European introductions. Several of these fossils consist of only a body whorl, lacking a shell spire. This damage pattern may indicate predation by rodents (Stokes 1917), and it is possible that these snails were carried into the cave by introduced rodents (most likely *Rattus rattus*) after the extinction of native rodents (Steadman and Ray 1982).

Deposition of land snails in fossil sites. — The snails probably entered the caves by several means. 1) Land snails commonly retreat into moist areas, including crevices and caves, during daily or seasonal dry periods. 2) Snails or their empty shells are washed into the caves with sediment influx during periods of extremely high rainfall. 3) Birds, rodents, or lizards may bring snails into caves as prey items. Most fossil shells, however, lacked damage patterns that might indicate such predation. An exception is *Naesiotus ochsneri,* discussed above. Snail shells were not present in owl pellets (*see* Mienis [1971] for a report of snail shells in pellets from the owl *Athene noctua* in Israel). 4) Snails entering the caves may have remained there to feed upon the accumulated bones and shells, which represent a rich source of calcium.

If some species of snails tend to feed on bones and shells more than others, then factor 4 may at least partially explain why some species and not others were found in cave deposits. Of the 51 species of land snails reported from Floreana or Santa Cruz or both, five have been recorded in the literature as having been collected on bones outside of caves — *Tornatellides chathamensis, Gastrocopta clausa, Gastrocopta munita, Succinea corbis,* and *Guppya bauri* (Dall 1896, Dall and Ochsner 1928). All but *Gastrocopta munita* are among the 16 species found as fossils in the present study. This suggests that at least some species may have entered and/or remained in the caves because of the accumulations of bone and shell inside. The numbers of species reported as occurring on bones versus those that have not falls short, however, of being significantly heterogeneous ($\chi^2_1 = 3.6346$, $P = .052$) between species found as fossils and all species recorded on Floreana and Santa Cruz. We have also identified fossil fecal strands from Cueva de Kubler that were probably left by one of the larger *Naesiotus* species, indicating that some snails were alive in the cave for at least a short time. To summarize, we believe that factors 1, 2, and 4 are important means of entry into fossil caves by snails, with factor 2 perhaps being especially important for the various species of *Naesiotus,* whose relatively sturdy shells are better able to withstand the rigors of sediment influx.

Comparison of fossil and historic snail faunas. — Essentially all fossil records are only subsets of the entire fauna being sampled, so it is expected that only a portion of the known land snail species from Floreana and Santa Cruz were found in the fossil deposits. On Santa Cruz, 15 species were found as fossils in or near deposits out of a reported total of 34 species in the historic fauna for that island (Dall 1900, 1917, Dall and Ochsner 1928, Pilsbry 1931, Odhner 1950, A. G. Smith 1966, 1972, Vagvolgyi 1977, Coppois and Glowacki 1983, this study). Of the historic fauna of 26 species on Floreana (Dall 1896, Dall and Ochsner 1928, Pilsbry 1931, A. G. Smith 1966), only three were found as fossils. On both islands, habitat preference probably accounts for many of these absences, for numerous species are known only from higher elevations than those of the fossil sites. We are not certain, however, why the Floreana fossil sites sampled the snail fauna so much more poorly than those of Santa Cruz, although perhaps the mode of sedimentary influx, especially the smaller sizes of the catchment basins on Floreana, is involved.

Among the species found as fossils on Santa Cruz, nine had not been reported from that island previous to A. G. Smith's visit in 1964. These are *Helicina nesiotica, Tornatellides chathamensis, Gastrocopta duncana, Succinea corbis, Guppya bauri, Habroconus? galapaganus, Retinella? chathamensis, Naesiotus kublerensis,* and *Naesiotus steadmani.* Except for *Succinea corbis,* which belongs to a taxonomically difficult

family, and the two *Naesiotus,* these are small snails that are no more than a few mm in their greatest shell dimension. A. G. Smith (1966) added new Santa Cruz records for all of these small species except *Gastrocopta duncana* and *Guppya bauri.* Our new records for *Gastrocopta duncana* and *Guppya bauri* consist, respectively, of only one and three shells.

Comparison of the fossil records of snails and vertebrates. —The distinction between historic faunas and paleofaunas is more difficult to discern with land snails than with vertebrates. Historic vertebrate faunas are based on specimens or field accounts taken of living individuals, whereas the historic land snail fauna of Galápagos is based largely on shell material, which under favorable conditions may persist intact and relatively unchanged for many years after the death of the animal. Thus the "historic" fauna may include species that were already extinct when first collected, and therefore we may be underestimating the extent of extinction in land snails. Historic faunas of snails therefore may be more representative of the natural (pre-human contact) fauna than are vertebrate faunas. In this respect, well-known historic faunas of land snails may be more appropriate subjects than birds and other vertebrates for tests of equilibrium ecological theories (*see* Solem [1982] for a recent study).

The fossil records of vertebrates from Floreana and Santa Cruz are more complete samples of the local fauna than those of snails. From both islands, the fossils included every species of terrestrial mammal or reptile, including those now extinct. The resident land bird faunas of Floreana and Santa Cruz are quite diverse (over 20 species), but the fossil record lacks only five species, three of which (*Neocrex erythrops, Coccyzus melacoryphus,* and *Dendroica petechia*) probably colonized Galápagos relatively recently, perhaps less than a thousand years ago (Steadman 1986). The fourth species, *Buteo galapagoensis,* is a large hawk that does not live in caves and is not preyed upon by barn owls; the absence of the fifth species, the owl *Asio flammeus,* can be accounted for in the same way.

The main reason that the fossil snails represent a much less complete sample of each island's local fauna is probably that the snails were not being concentrated in the caves by predators. Therefore, unlike the vertebrates that were being sampled within approximately a 1 km radius of the cave (the estimated home range of the barn owl *Tyto punctatissima*), only the snails that lived in the immediate vicinity of the caves had an opportunity to be deposited within the caves.

Vertebrate extinction in the late Holocene of Galápagos occurred mainly or entirely in historic times, and can be related circumstantially to human-related impacts. Such impacts, especially habitat disturbance, may have affected the present snail faunas. In contrast to some cases of vertebrate extinction in Galápagos, direct human predation is an unlikely factor in land snail declines. The detrimental, often catastrophic, effects of land clearing for agriculture and of introduced mammals on land snail faunas on Pacific islands and elsewhere, however, has been noted repeatedly (e.g., Solem 1974, 1976, Christensen and Kirch 1981*a, b,* Wells et al. 1983, Neck 1984). Agricultural conversion has very likely been detrimental to Galápagos land snails on Floreana, the island in the archipelago with the longest history (beginning early in the 19th century) of human settlement (Slevin 1959). Santa Cruz was not settled until the present century, but is now the most heavily populated and visited island, and much of the southern part, including areas near the fossil localities, has been converted to agricultural uses (Schofield 1973).

Introduction of exotic organisms, especially mammals, is probably the most pervasive human-caused threat to the native land snails in Galápagos. Feral goats (*Capra hircus*), cattle (*Bos taurus*), donkeys (*Equus asinus*), pigs (*Sus scrofa*), dogs (*Canis familiaris*), and cats (*Felis catus*) have lived or are living on both Floreana and Santa Cruz; and goats, cats, and donkeys remain common today in the vicinity of the Floreana fossil sites (Steadman 1986). Cats and dogs probably had no effect on snails, but cattle, donkeys, pigs, and especially goats can destroy land snail habitat by removing or altering native plant communities through persistent grazing and browsing (Weber 1971, Hamann 1975). Pigs have the additional destructive habit of rooting through

litter and soil; this turning over of the substrate can kill snails directly and, more importantly, exposes moist, subsurface refuges to desiccation. Rooting pigs may also eat snails that they encounter.

Introduced rats (*Rattus rattus*) and mice (*Mus musculus*) are present in Galápagos. Rodent-gnawed shells have been found on islands that have declining land snail faunas (e.g., Stokes 1917). Although predation by introduced rodents on land snails is extremely likely, it is possible that in some cases they gnaw already dead shells for calcium, as they sometimes do on vertebrate bone. Interactions between rodents and living land snails deserve intensive investigation. Indications of rodent predation on Galápagos fossils are limited to *Naesiotus ochsneri,* as discussed earlier.

Although detrimental effects have yet to be reported, introduced snails have been recorded from Galápagos (Smith 1966). Replacement of native land snails by introduced snails has been noted on islands elsewhere (Solem 1974, Christensen and Kirch 1981*a, b*), although it is sometimes not clear if these cases involve direct competition and replacement or simple occupation by introduced snails of human-modified habitat that has become unsuitable for native species. The introduced predatory snails that have proven so catastrophic to other island land snail faunas (Hadfield and Mountain 1980, Clarke et al. 1984) have not yet made an appearance in Galápagos. Introduced ants (Lubin 1984) are also potential predators on native land snails (Solem 1976).

Although direct evidence of impacts of humans and introduced mammals is lacking, except for possible rodent predation, there are a number of indications that such influences exist. Despite the efforts of Ochsner in 1905–1906 and A. G. Smith in 1964, *Gastrocopta duncana* and *Guppya bauri,* both reported here as fossils, were not previously reported from Santa Cruz. *Naesiotus cymatias, N. ochsneri, N. blombergi,* and many of the smaller species found as fossils have been reported from historic collections on Santa Cruz, although generally from higher elevations than the fossil sites. *Naesiotus kublerensis* and *Naesiotus steadmani* are known only from limited shell material and may be extinct. *Naesiotus cymatias* on Santa Cruz and *Naesiotus galapaganus* on Floreana are rare in historic collections, but both are ubiquitous and extraordinarily abundant as fossils.

Dall long ago warned of the vulnerability of the Galápagos land snail fauna, citing gaps in the understanding of the Hawaiian fauna "because the sheep and goat have preceded the investigator" (Dall 1896:29). Dall's warning was repeated by A. G. Smith (1966). The DeRoy family, which has lived on Santa Cruz since 1958, has told DWS (*personal communication* 1978, 1980) that it is much more difficult to find living examples of most land snails today on Santa Cruz than it was only two decades ago. Coppois and Glowacki (1983) made the general observation (supported in Coppois [1984]) that some Santa Cruz bulimulid snails "are extinct or on their way to extinction." Extinction is difficult to prove in these land snails because living snails can be overlooked owing to their inconspicuous color, size, and habits. Regardless, there are clear signs of reductions in range and abundance.

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